Effect of Silhouette Color on Trap Catches of *Dendroctonus frontalis* (Coleoptera: Scolytidae)

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ABSTRACT With the exception of responses to semiochemicals, host selection behaviors of *D. frontalis* are largely unstudied. To better understand the host finding behavior of *D. frontalis*, and to identify potential visual disruptants, we evaluated the response of *D. frontalis* to multiple-funnel traps of eight different colors. Multiple-funnel traps provide an attractive vertical silhouette, similar to a host stem, that aids in capturing bark beetles and allows for controlled evaluation of visual cues. Evaluation of mean trap catch of each color by analysis of variance (ANOVA) produced two separate groups: white and yellow traps caught significantly fewer *D. frontalis* than the other six colors tested (black, blue, brown, gray, green, red). Examination of spectral reflectance curves showed that the eight colors could be naturally placed into two groups, those with high peak reflectance (white and yellow) and those with low peak reflectance (black, blue, brown, gray, green, red). When high and low peak reflectance were substituted for color in a separate ANOVA, reflectance group was as good as color at explaining the variability in trap catch ($r^2 = 0.88$ versus 0.92). Therefore, hue (dominant wavelength) was unimportant in affecting *D. frontalis* host finding behavior at the reflectance levels we tested and, thus, we found no strong evidence that differential wavelength sensitivity affected the response of *D. frontalis*. These results show that dark colored silhouettes (those with low reflectance values), regardless of hue, are best for capturing *D. frontalis*, while white or yellow are the best candidate colors for disrupting host finding.

KEY WORDS bark beetles, southern pine beetle, Scolytidae, host finding, insect vision

HOST SELECTION BY insects is a complex process in which each of five steps (host-habitat finding, host finding, host recognition, host acceptance, host suitability) must be completed in ordered sequence for a host to be successfully used (Kogan 1994). Because multiple sensory systems operate during host selection (Thorsteinson 1960, Miller and Strickler 1984, Kogan 1994), a number of variables may disrupt the process, thereby preventing its completion. Behaviors during host finding are typically dominated by responses to visual and olfactory cues (Kogan 1994). In those species for which pheromones have been identified, research on host finding, and its disruption for management, usually concentrates on semiochemicals and related olfactory behaviors and physiology (e.g., Cardé and Minks 1997). Vision, however, often impacts host finding by insects (Prokopy and Owens 1983, Allan et al. 1987, Judd and Borden 1991, Kogan 1994) and, especially when combined with olfaction, may produce effects that determine whether or not host finding is completed successfully.

In scolytids, host finding is primarily a prelanding phenomenon, being completed before host recognition, which apparently requires gustation (Elkinton and Wood 1980). While olfaction is considered para-

mount for host finding (Borden 1993, 1997), vision also is recognized as important (Shepherd 1966, Payne and Coulson 1985, Borden et al. 1986). Indeed, when visual stimuli are incorporated into management tactics for bark beetles, their effectiveness often is increased. For example, traps that provide appropriate visual silhouettes (Lindgren et al. 1983, Fatzinger 1985, Chenier and Philogene 1989, McCravy et al. 2000) are usually more efficient, and control measures for tree-killing species are thought to be more effective when they reduce nearby, visually-attractive stimuli through tree removal (Billings 1980, Salom et al. 1997, Clarke et al. 1999). Therefore, visual cues are known to play a role in scolytid host selection behaviors, but their relative importance has yet to be elucidated.

True color vision has been demonstrated only for a limited number of insect species, and has not been demonstrated in the Scolytidae (Menzel and Backhaus 1991). By far the most studied insect in this regard is the honey bee, *Apis mellifera* L., because of its importance in agriculture, and because it is amenable to training. Proof of color vision requires that the animal be trained, making it difficult to demonstrate in many insect species (Menzel and Backhaus 1991). Therefore, the lack of demonstrated true color vision in the Scolytidae does not mean that they cannot distinguish colors. On the contrary, electroretinograms (ERG's) have demonstrated differential wavelength sensitivity in the eyes of at least two species, *Dendroctonus pseudotsugae* Hopkins and *Ips paracon-*

fusus Lanier (Groberman and Borden 1982). At the whole-insect level, a walking assay with *D. pseudotsugae* and *Trypodendron lineatum* Olivier in the laboratory (Groberman and Borden 1981) produced variable responses at different wavelengths. Taken together, these studies suggest that scolytids have the physiological capability for at least dichromatic vision and that colors may affect behavior.

Several field studies have evaluated the response of scolytids to colored traps. Both *D. ponderosae* Hopkins and *Ips montanus* (Eichoff) responded variably to traps of different colors, with lighter colors catching fewer individuals than darker colors (Schönherr 1977). Lindgren et al. (1983) found that the ambrosia beetles, *T. lineatum*, *Gnathotrichus sulcatus* (LeConte), and *G. retusus* (LeConte) were not affected by trap color. These results are supported by Dubbel et al. (1985), who observed that *T. lineatum* and *I. typographus* (L.) were unaffected by any color tested except white (not tested by Lindgren et al.), which caught ≈53% fewer *T. lineatum* and 66% fewer *I. typographus* than black. In contrast, Niemeyer (1985) found that white traps caught more *I. typographus* under certain conditions, a result apparently dependent upon habitat and trap distance. The cone beetle, *Conophthorus resinosae* Hopkins, was unaffected by trap color, even those with high peak reflectances (de Groot and Zylstra 1995). Other species of scolytids are typically quite responsive to colors. For example, catch of *Dendroctonus* spp. and *I. montanus* was significantly reduced by bright colors (Schönherr 1977, Strom et al. 1999), and the southern pine beetle, *Dendroctonus frontalis* Zimmermann, was significantly affected by white traps (Strom et al. 1999). Relative to black, white multiple-funnel traps caught ≈70% fewer *D. frontalis* than black, and white sticky panels reduced catch by 79%.

Increased knowledge of the cues and stimuli involved in host selection would likely facilitate more effective management strategies. For example, pheromone-based monitoring programs for *D. frontalis* use multiple-funnel traps, which provide an attractive visual silhouette similar to a host, and the antiaggregation pheromone, verbenone, is more effective when applied in conjunction with tree felling, which removes nearby visual silhouettes (Billings 1980, Salom et al. 1997, Clarke et al. 1999). Although visual disruption of *D. frontalis* host selection has recently been demonstrated (Strom et al. 1999), colors other than black and white have not been evaluated for their effects. In addition, there is currently no adequate means to predict the potential of various colors to disrupt host finding of *D. frontalis*, because visual physiology and behavior of the beetles are unstudied. Thus, the most reasonable way to describe the generality of visual responses–which, eventually, may allow more effective use of visual stimuli in monitoring or manipulation strategies–is to directly evaluate selected silhouette colors using traps. Therefore, the objectives of this experiment were to evaluate the response of *D. frontalis* to a variety of colors, and to determine the relative effect of these visual silhouette
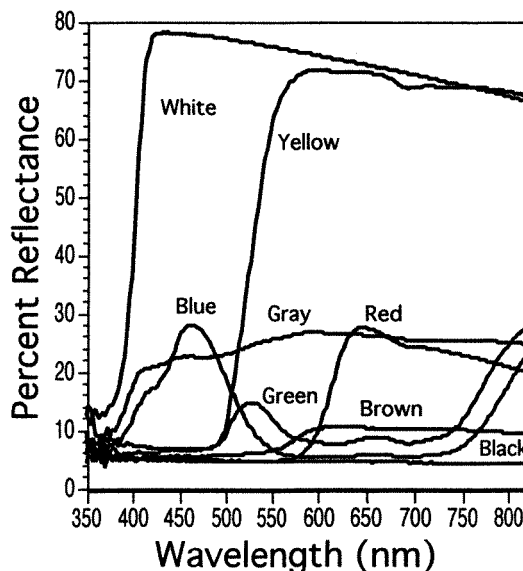

Fig. 1. Reflectance spectra of traps painted with various colors of Krylon spraypaints. The spectrum of each color is its reflectance relative to a white standard (99% pure Spectralon calibrated reflectance standard).

modifications on the host finding behavior of this beetle.

Materials and Methods

This study was conducted in Florida during May and July 1997 and consisted of seven replicates, one at each of seven sites. All sites were plantation pine (12–20 yr old), six loblolly, *Pinus taeda* L., and one slash, *Pinus elliottii* Engelm., each with an active *D. frontalis* infestation. Multiple-funnel traps were used, because they provide physical stimuli that are similar to tree boles, making them reasonable host mimics and good models for host finding. At the same time, they reduce spatial and temporal variations that are inherent in pine hosts, allowing treatments to be compared more directly. Eight traps, one of each color, were assigned initial positions at random, 5–10 m apart, then rotated each day either systematically (three sites) or reassigned positions randomly (four sites), depending upon the length of time a site was available before harvesting (i.e., sites cut in fewer than 8 d were sampled using the latter method). Mean trap catch of each color at each site was used as the dependent variable in all analyses.

Visual treatments consisted of multiple-funnel traps (16-funnel; Phero Tech, Delta, BC, Canada) painted with various colors of Krylon spray paints (Krylon, Division of Sherwin-Williams, Solon, OH) (Fig. 1). The colors used were: gloss black (Krylon product number 1601), true blue (no. 1910), leather brown (no. 2501), dove gray (no. 1605), moss green (no. 2004), cherry red (no. 2101), gloss white (no. 1501), and sun yellow (no. 1806). Other than color pigments,

the different colors of Krylon paints do not use different ingredients (Krylon, Inc.), thus controlling for potential semiochemical effects among paint colors. Reflectance spectra (Fig. 1) were generated for each color by comparing it to a white standard (Spectralon SRS-99–010 calibrated reflectance standard; Labsphere, North Sutton, NH) using a Labsphere RSA-SP-84 integrating sphere attachment on a Hewlett–Packard HP 8452A diode array (UV:VIS) spectrophotometer. All traps were baited with the attractive semiochemical blend frontalure (2 parts alpha-pinene to one part frontalin) ($\approx$2.5 ml) eluted from transfer pipettes (4 ml; Corning Samco Corporation, San Fernando, CA) (Strom et al. 1999). Field elution rates were determined previously to be 46–58 mg/d, depending on light environment (lower values in the shade, higher in full sun) but independent of trap color (black or white) (Strom et al. 1999).

Data were analyzed by mixed-model (sites considered random) ANOVA (Proc Mixed) (SAS Institute 1997), with the mean daily catch for each color at each site, transformed by its natural log, serving as the dependent variable. Mean separations were accomplished using Tukey's studentized range test (SAS Institute 1997). Histograms of raw data (Proc Univariate) (SAS Institute 1997) and visual inspection of residuals demonstrated that transformed values better met the assumptions of parametric statistics. The effect of color on catch of *D. frontalis* was evaluated using the ANOVA model: catch = site, color. Because a plot of peak reflectance suggested that there were two distinct groups in our treatments, one with relatively low peak reflectance (six colors) and one with high peak reflectance (white and yellow) (Fig. 1), a second ANOVA was used to evaluate this parameter. The effect of peak reflectance group (high or low) was evaluated using the model: catch = site, peak reflectance group. This model was more parsimonious because it used only 1 degree of freedom for treatment effects (compared with seven for color) and eliminated the effects of hue (at the reflectance levels of our colors).

Results

Each color had a unique reflectance spectrum, showing the effects of hue (the wavelength at which a peak occurs), intensity or peak reflectance (how high the peak reflectance was), and saturation (unsaturated colors are those without a distinct hue, i.e., black, gray, and white) (Fig. 1). The peak reflectance of white and yellow traps was >70%, and, above $\approx$500 nm, their spectra were similar. Other colors differed in hue but had similar peak reflectances, all being <30%.

More than 370 trap collections were made, resulting in a total catch of >101,000 *D. frontalis* during the 20 trapping days of this study. Mean catch of *D. frontalis* was significantly affected by trap color ($F = 21.62$; df = 7, 42; $P < 0.0001$). White and yellow traps caught significantly fewer *D. frontalis* than any other color ($P < 0.05$ in all cases) (Fig. 2). There were no significant differences in catch among the other six colors
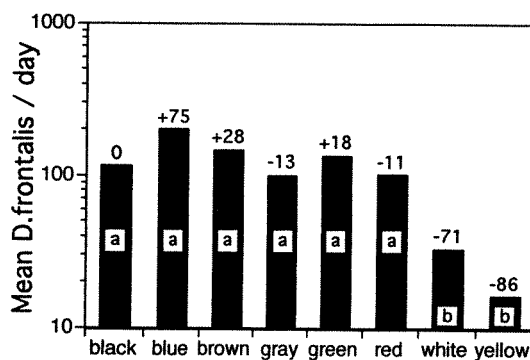

Fig. 2. Mean catch of *D. frontalis* in multiple funnel traps of each color. Means are adjusted for differences in the number of *D. frontalis* caught among seven sites (least-square means) and back-transformed from natural logs following ANOVA. Numbers above bars give the percentage change relative to black. The fit of the ANOVA model was very good ($r^2 = 0.92$), making the standard errors of each least-square mean relatively small (SEM = 1.64). Bars with different letters are significantly different ($P < 0.05$, Tukey's studentized range test).

($P > 0.05$). The average percent reduction of *D. frontalis* in white and yellow traps compared with black was 71 and 86%, respectively (Fig. 2). Catch in yellow versus white traps was not significantly different ($P > 0.05$). This result suggests that the greater reflectance of white in the wavelength range from 400 to 500 nm (Fig. 1) was unimportant for *D. frontalis* behavior.

Further exploration of our trap colors using reflectance spectra (Fig. 1) revealed that they could be grouped into those with high peak reflectance and those with low peak reflectance (Fig. 3). At these reflectance levels, hue had no effect on the number of *D. frontalis* caught; rather, peak reflectance (i.e., the peak reflectance without regard to dominant wavelength) explained nearly the entire visual effect. When reflectance group (high or low) was substituted for color in the ANOVA model, the result was virtually unchanged (r^2 of 0.88 versus 0.92 for the model with color) (Proc GLM) (SAS Institute 1997). Across sites, catch of *D. frontalis* in traps with low peak reflectance ($\bar{x} = 128.4$) was significantly higher than those with high peak reflectance ($\bar{x} = 23.1$) ($F = 105.9$; df = 1, 48; $P < 0.0001$). Substituting peak reflectance for color in the ANOVA model resulted in virtually no change in model fit, but provided a more parsimonious explanation for the observed effects. Although no reflectance levels intermediate to the two groups were evaluated (i.e., between 30 and 70% peak reflectance), it appears that hue, in the visual range at these reflectance levels, did not affect host finding of *D. frontalis*.

Discussion

The significant reduction in the number of *D. frontalis* caught by white and yellow traps compared with the other six colors ($\approx$80%) demonstrates that both colors hold potential for successful disruption of host
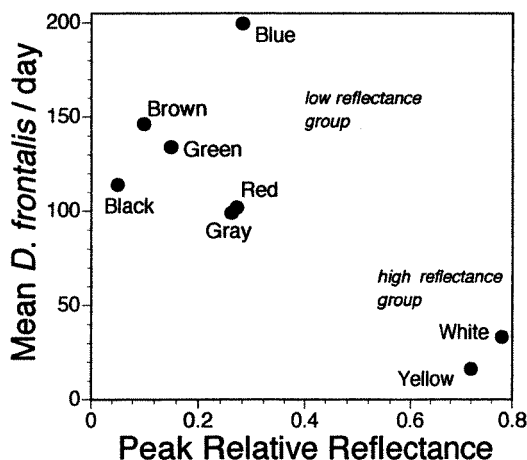
Fig. 3. Mean catch of *D. frontalis* and the peak reflectance, relative to a white standard, of each color. Peak reflectance of each color was obtained from Fig. 1, mean catch of *D. frontalis* from Fig. 2. Two groups are recognized, a high reflectance group consisting of white and yellow, and a low reflectance group including black, blue, brown, gray, green, and red. The high reflectance group caught significantly fewer *D. frontalis* than the low reflectance group ($P < 0.0001$), while there were no differences observed within each group ($P > 0.05$).

finding of this beetle and suggests that either would be a good choice for further evaluation and development as visual disruptants. The reduction in the number of *D. frontalis* caught in white traps compared with black in this experiment was very similar to that observed earlier with multiple-funnel traps ($\approx 70\%$) and sticky panels (79%) (Strom et al. 1999). Thus, modification of visual silhouettes using bright (high reflectance) colors provides both consistent and significant reductions in the number of *D. frontalis* trapped.

The results also show that, in the visual range (400–700 nm), hue was unimportant for capturing *D. frontalis* at the reflectance levels tested. Among the six colors categorized as low reflectance (Fig. 3), none showed significant variability in the number of individuals caught (Fig. 2). Comparing white and yellow it is interesting to note that, although no significant differences in catch were observed, yellow traps caught the fewest *D. frontalis* at every site. Either white or yellow appears suitable for disruption of *D. frontalis* host finding, while any of the other colors could be used in monitoring or management schemes where the objective is to attract as many *D. frontalis* as possible.

The visual physiology of *D. frontalis* has not been studied; however, there are two bark beetle species, *D. pseudotsugae* and *I. paraconfusus*, whose electrophysiological responses to light have been evaluated using ERGs (Groberman and Borden 1982). The response of each of these species was similar, with two sensitivity maxima being observed in the visual range: one in the blue region (≈ 450 nm) and one in the green (510–530 nm). By comparison, we did not observe any effects

that suggest *D. frontalis* had strong positive or negative responses at either of these wavelengths, i.e., neither blue nor green traps caught significantly different numbers of *D. frontalis* than the other colors in the low reflectance group (Figs. 1 and 2). It is possible, perhaps likely, that scolytids possess a third sensitivity maximum in the UV (UV) range, but experiments with UV light have not been conducted and neither attraction nor disruption of *D. frontalis* host finding seems to require it. The results of this experiment support the idea that UV reflectance is unnecessary to disrupt host finding of *D. frontalis*, as white and yellow traps, neither of which reflected much UV (Fig. 1), reduced trap catches by >70%. Apparently UV reflectance is not necessary for attraction of *D. frontalis* either, because boles of southern pines, their natural hosts, do not reflect much UV (Strom et al. 1999).

The reflectance spectrum of an object *in situ* is a function of its reflectance potential and the availability of light across the electromagnetic spectrum. Our laboratory results provide a high quality relative measure of reflectance, but our methods do not allow us to evaluate the actual reflectance of traps in the field. Published measures of light quality in southern pine forests are scant. Hailman (1979) observed that, under cloudy conditions, closed canopy loblolly pine forests reduce total light by about an order of magnitude but change light quality very little. Under sunny conditions, closed forest canopies (forest shade) reduce total light and cause a color change from whitish to yellow-green, with one peak of transmittance at ≈ 550 nm and another in the red range above 680 nm (Endler 1993).

Strom et al. (1999) hypothesize that *D. frontalis* is a 'visual specialist', which implies that it should be relatively easy to disrupt with visual treatments (*sensu* Prokopy and Owens 1978). Ease of disruption may be taken to mean that any variation from the visual stimulus provided by the natural host should disrupt host finding or, alternatively, that a disruptant stimuli, when it exists, should be more effective. Although this hypothesis was not directly addressed in this experiment, the results support the latter interpretation. No color other than white or yellow negatively affected host finding of *D. frontalis*. However, the results of this and other experiments suggest that some species of scolytids are not affected by visual stimuli (e.g., *Conophthorus resinosae*, *Gnathotrichus*, spp.), while others are significantly deterred by white silhouettes (e.g., *Dendroctonus* and *Ips* species). Among the species of scolytids that have been tested, *D. frontalis* seems to exhibit the most dramatic difference between white and black traps. Modification of visual silhouettes using highly reflective (>70% of the standard) white or yellow paint consistently reduces successful host finding (landing) of *D. frontalis* by 70–90%. Therefore, *D. frontalis* is a likely candidate for which to evaluate strategies that include manipulation of the visual environment to more efficiently meet management objectives.

The utility of employing color, for either disruption or attraction, will not be known for certain until field

experiments are done to test management scenarios of interest. The levels of visual disruption observed with *D. frontalis* are, however, as great or greater than those achieved thus far from antiaggregant semiochemicals (Salom et al. 1992, Hayes et al. 1994), some of which are now available to managers. In addition, visual and olfactory disruption appear additive in *D. frontalis* (Strom et al. 1999), suggesting that more effective protectants may be developed through disruptant combinations. Therefore, increasing our knowledge of the biology and ecology of scolytid host selection may be a fertile area for facilitating both the improvement of existing management strategies as well as the development of novel ones.

Acknowledgments

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